

THE PLEISTOCENE RODENT *ALTERODON MAJOR* AND THE MAMMALIAN BIOGEOGRAPHY OF JAMAICA

by R. D. E. MACPHEE, C. A. WOODS and G. S. MORGAN

ABSTRACT. The putative Jamaican octodontid rodent *Alterodon major* is based on a single cheek tooth. Restudy of this specimen indicates that it is probably incomplete, and that it is much more likely to represent a heptaxodontid than an octodontid. If this inference is correct, then there is no longer any reason to believe that there was an independent octodontid invasion of Jamaica. Although this clears up one biogeographical puzzle, no new light is shed thereby on the origins and dispersals of Caribbean land mammals. Jamaica occupies a key position in island-hopping models, but virtually nothing is known of the mammalian palaeontology of this island. Further investigations are clearly indicated.

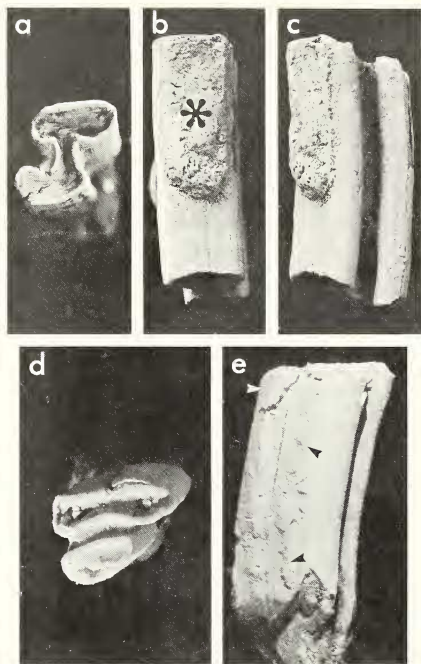
ALTERODON MAJOR, a fossil hystricognath rodent usually assigned to Octodontidae (e.g. Anthony 1926; Winge 1941; Simpson 1945; Landry 1957), is based on a single cheek tooth recovered from a Jamaican cave breccia of presumed latest Pleistocene or Holocene age (Anthony MS, 1920). The presence of this rodent in the Greater Antilles is difficult to explain, since octodontids are otherwise restricted to the southern part of South America (Simpson 1956; Wood and Patterson 1959). If correctly allocated, this specimen has significant implications for current theories regarding the minimum number of separate invasions required to explain the composition of the Caribbean rodent fauna (Woods and Howland 1979).

In the course of other work each of us has had the opportunity to examine the type of *Alterodon*, and each of us has concluded that it does not represent an octodontid. Others (e.g. S. B. McDowell *vide* Simpson 1956) have reached the same conclusion, but no previous researcher has formally reassessed *Alterodon*'s validity or proper allocation. This we undertake here, together with a short reassessment of the mammalian biogeography of Jamaica.

Institutional abbreviations used in the text and figures are: AMNH (American Museum of Natural History), FSM (Florida State Museum), and NRCDC (Natural Resource Conservation Department, Ministry of Mining, Government of Jamaica).

ALLOCATION OF *ALTERODON MAJOR*

The holotype (AMNH 17638) of *Alterodon major* is anatomically simple, consisting of two unequal laminae united by a narrow bridge (text-fig. 1a-c). The occlusal surface is reminiscent of the numeral 8—hence Anthony's *nomen*, a strophe on the Greek for 'dumb-bell'. The cores of the laminae are dentine, and their enamel casing is continuous and uncomplicated. The pulp cavity of the tooth is exposed, indicating that the tooth was unrooted. In all of these details of construction AMNH 17638 is indeed superficially similar to the bilobate or bilaminar configurations characteristic of non-acaremyine octodontid cheek teeth, as Anthony asserted in his comparisons. However, his diagnosis cannot be accepted at face value, because the specimen is almost certainly incomplete. Anthony (1920, p. 475, fig. 4) illustrated, but did not comment on, a thick layer of cementum on an exposed surface of the type's larger lamina. This layer is roughened and damaged (text-fig. 1b, c), suggesting breakage and perhaps the loss of some substantial portion of the original tooth. How much was lost is of course uncertain, since the specimen is unique. However, the simplest explanation for the specimen's present appearance is that the tooth was originally composed of



TEXT-FIG. 1. Holotype (AMNH 17638) of *Alterodon major* (a, b, c), compared to an incomplete cheek tooth of a specimen (AMNH 108554) referred to *Clidomys parvus* (d, e). Views are a, d, occlusal; b, distal; and c, e, ?distolateral. Asterisk in b identifies cementum plaque; remnants of homologous plaque can be seen on *C. parvus* specimen (e, pointers). Other specimens of latter tooth possess three laminae. About $3.5 \times$.

several laminae, welded together by plaques of interstitial cementum. One or more of these laminae spalled off during the deposition process, thereby considerably altering the tooth's size and complexity. Multilaminar, cementum-bound cheek teeth are moderately common in Hystricognathi; depending upon species, such teeth may consist of three to thirty (or more) lamina-plaque units. But teeth of this sort are *not* found among known Octodontidae, with the single egregious example of *Alterodon*. If we are correct in our interpretation that this tooth is incomplete, then the basis for Anthony's allocation disappears and *Alterodon*'s proper taxonomic placement must be sought elsewhere.

We tried but failed to find a match for AMNH 17638 among extant and extinct hystricognath genera restricted to South and Central America. Fugitive resemblances to non-Antillean families with multilaminar teeth (e.g. members of Dinomyidae) were neither detailed enough nor numerous

enough to warrant serious consideration. Families presently or previously resident in the Caribbean (Table 1) are obvious choices for *Alterodon*'s source, but of these the only likely candidates are Capromyidae and Heptaxodontidae. The native capromyid of Jamaica is *Geocapromys* (coney or hutia), but the sole specimen of *Alterodon* is clearly too large and too morphologically divergent to represent that genus. The same conclusion applies to other capromyid genera distributed elsewhere in the Caribbean. *Alterodon* is, however, well within the size range of heptaxodontids, and two facts justify the conclusion that *Alterodon* is almost certainly a member of this latter group even though precise allocation remains elusive.

TABLE 1. Distributions of Land Mammal Families in the Greater Antilles*

	Jamaica	Cuba	Hispaniola	Puerto Rico
Solenodontidae		×	×	
Nesophontidae		×	×	×
Cebidae			×	
Atelidae	×			
Megalonychidae		×	×	×
Cricetidae	×			
Heptaxodontidae	×		×	×
Capromyidae	×	×	×	×
	4-5	8-10	11-12	5-7

* The status and affiliation of several Antillean genera are currently in doubt and the subject of some disagreement among ourselves. In constructing this table, decisions about family limits and contents were made by consensus, in the following manner. Solenodontidae, Nesophontidae, Megalonychidae, and Cricetidae are defined and distributed as in Simpson's (1956) paper. *Xenothrix* (Williams and Koopman 1952) is a pitheciine atelid according to Rosenberger's (1977) cladogeny, and not a cebid unless one chooses to group all New World monkeys in a single family. Cebidae *sensu stricto*, however, do occur in Hispaniola (Rimoli 1977; MacPhee and Woods 1982). Heptaxodontidae may not be monophyletic (Ray 1964, 1965), but pending further study we retain the accepted form of this family (and include *Quemisia*). The coypus and the spiny rats of the Caribbean are usually regarded as being members of separate families (Capromyidae and Echimyidae respectively), but Woods (in press) argues that they are in fact sister groups and should probably be included in a single family (Capromyidae). The sister group of this latter taxon consists of non-Antillean echimyids (i.e. those living in South America).

Precise generic counts are not feasible at this time; the stated ranges are probable maxima and minima. Historical introductions (e.g. *Herpestes* in Jamaica) are omitted.

First, no other putative octodontid fossil has been found at *Alterodon*'s type locality—Wallingford Roadside Cave—but heptaxodontids have, and in abundance. This is of some importance, because nothing else has come out of Wallingford except coney bones and the remains of various reptiles. (Wallingford Roadside Cave is, in fact, the type locality of all of Jamaica's nominal heptaxodontid species, and is the only site on the island where their remains are frequent in 'bone breccias'.) In a recent collecting trip one of us (R.D.E.M.) spent several days at Anthony's old excavations at Wallingford and freed about seventy fossils from the breccia coating the cave's walls. Not one of them proved to be allocatable to Octodontidae. We doubt that inadequate sample sizes can explain the lack of new material of *Alterodon*.

The second reason for suspecting that *Alterodon* is really a heptaxodontid is based on preferential fracturing patterns of rodent teeth. Heptaxodontid cheek teeth, which consist of three or four laminae completely separated by cementum plaques, tend to fracture cleanly at enamel-cementum boundaries. Teeth which do not consist of completely independent lamina-plaque units are more likely to crumble or to fracture raggedly when force is applied to a selected point. Signs of

damage are usually obvious in the second case, but may not be in the first. In museum collections of heptaxodontids one can find numerous examples of isolated whole laminae which retain patches of cementum on their mesial or distal surfaces (text-fig. 1*d, e*); the gross resemblance of these partial teeth to the *Alterodon* specimen is obvious. Without forcing the available evidence beyond its limits, the following series of conclusions seem justified: if AMNH 17638 is incomplete, *Alterodon* cannot be an octodontid; if the specimen does not represent some heretofore unknown group of New World rodents, *Alterodon* is probably a member of some radiation native to the Greater Antilles; and in view of the island and place of its discovery, membership most probably lies with Heptaxodontidae.

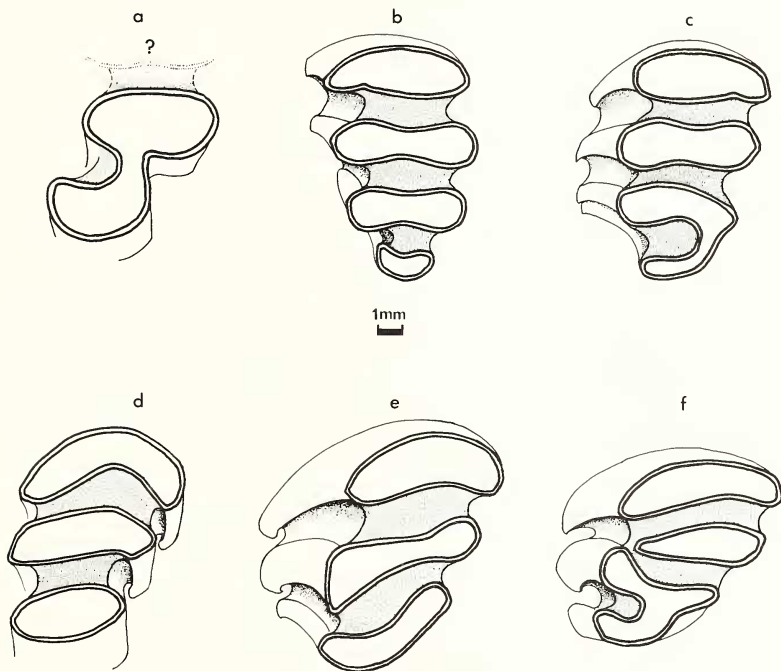
Although we adopt the view that *A. major* is a heptaxodontid, its condition is such that we cannot place it precisely within the group. The holotype may represent a distinct genus or species, or it may be no more than an individual variant of some other recognized taxon. In favour of the first option is the fact that no tooth or tooth fragment in the collections of the AMNH, FSM, or NRCDC exactly conforms to AMNH 17638 (although some come close; see text-fig. 2). Supporting the second interpretation is the fact that reinvestigation (MacPhee, in prep.) of all available specimens of Jamaican heptaxodontids reveals that Anthony (1920) seriously misevaluated their within-group variability. Although there is considerable variation in size within the group, distributions are distinctly bimodal for most measurable traits, and there is no good reason to recognize more than two species (of one genus) in taxonomically partitioning the sample. (Anthony recognized four, which he distributed among three genera.) Pending proposed revision of Heptaxodontidae, it seems best to recognize *A. major* as an additional species, but with the caveat that it may represent no more than an individual variant of *Clidomys* (the genus name having page priority in Anthony [1920]). The resemblance of *Alterodon* to other heptaxodontids of the West Indies (Table 1) is no greater than one would expect in distant members of the same family, and there is no compelling reason to believe that *Alterodon* and *Clidomys* derive from different ancestries within Heptaxodontidae.

MAMMALIAN BIOGEOGRAPHY OF JAMAICA

The most obvious effect of including *Alterodon* within Heptaxodontidae is that Jamaica's known faunal diversity, already meagre, is reduced by one family. The non-chiropteran mammals compose a truly depauperate brigade—one species each of Capromyidae (*Geocapromys brownii*), Cricetidae (*Oryzomys antillarum*), and Atelidae (*Xenothrix mcgregori*), and an indefinite but surely small number of heptaxodontids. Exclusion of Octodontidae from this list leaves Jamaica with the smallest range of land mammals of any of the Greater Antilles (Table 1).

Unfortunately, recognition of the probable affinities of *A. major* does not shed any new light on the vexed question of the origins and subsequent fate of the Antillean land mammal fauna. Most students still prefer the dispersionist argument espoused by Matthew (1918), Darlington (1938), Simpson (1956), Pregill (1981), and others, which specifies that the distribution of Caribbean mammals (and many other organisms) can be most parsimoniously explained as the concatenation of many independent immigration events. This explanation assumes that Antillean populations were founded exclusively by waifs, which were able to disperse from circumjacent mainlands or previously occupied islands by riding on rafts of natural vegetation and suchlike vehicles (e.g. palm-frond 'boats'). Dispersal mechanisms of this sort are rejected as improbable by proponents of the vicariance hypothesis of Caribbean biogeography (Rosen 1976, 1978; see also general discussion in Nelson and Rosen 1981). Vicarists, however, propose the no less improbable thesis that the big islands have drifted out into the Caribbean Sea carrying nearly their entire native fauna with them. While it is likely that plate motions have indeed affected the relative positions of these islands, the scope of these movements appears to have been much less than required by the vicarist scenario (Pregill 1981). In any event, since the islands have been in approximately their present locations for most of the Cenozoic, the pertinence of plate tectonics to understanding the origins of Caribbean mammals appears to be slight.

Jamaica's role (if any) in ancient faunal movements within the West Indies is quite uncertain. In its faunal composition Jamaica differs sharply from Cuba, Hispaniola, and Puerto Rico in lacking insectivores and sloths (Table 1). Its apparent biotic isolation from the other Greater Antilles is further emphasized by the distinctiveness of *Xenothrix* and *Clidomys* (and *Alterodon*) within their respective families, which in turn implies lengthy separations from their supposed Caribbean-Neotropical relatives (Rosenberger 1977; MacPhee and Woods 1982). Indeed, as regards Jamaican



TEXT-FIG. 2. Comparison of occlusal surface organization in *Alterodon* (a, AMNH 17638) and selected Jamaican heptaxodontid teeth (semischematic). One possible match for the *Alterodon* holotype is the tetralaminar tooth illustrated in b (AMNH 108557, *Clidomys parvus*), which Anthony (1920) regarded as the ?M³ of *Clidomys* sp. The two distal laminae of the putative M³ (no *in situ* specimens are known) are continuous in some specimens of this tooth (e.g. c, AMNH 17635, holotype of '*Spirodonomys jamaicensis*' Anthony 1920). An alternative match is M₃ of *Clidomys* sp. (e.g. d, AMNH 108543), although no (other) examples of laminar bridging at this locus have been found. Another possibility is the permanent P₄, often highly variable in hystricognath species. Among heptaxodontids a simple trilaminar configuration is typical for P₄ (e.g. e, AMNH 108556), but more elaborate versions are also found (f, FSM 27438). Non-Jamaican heptaxodontids exhibit premolar replacement, and it is likely that the same was true for the Jamaican forms. We cannot exclude the possibility that AMNH 17638 is a *deciduous* premolar of *Clidomys* (which may account for its rarity in existing collections).

mammals (other than bats), the only native genus found on at least one other island is *Geocapromys* (in Cuba and several offshore islands). Since the original centre of capromyid dispersion was probably in the eastern rather than the western Caribbean (Woods, in press), *Geocapromys* in all likelihood crossed into Jamaica from Cuba rather than vice versa. These points could be interpreted as an indication that Jamaica has been a faunal backwater which received only a small handful of land mammal immigrants during the late Cenozoic, and that most dispersal events and interchanges occurred among the islands to the north and east. However, another possibility exists. Jamaica is advantageously placed for receiving immigrants from Central America and northern South America, and despite vicarist reservations it is not unreasonable to believe that this geographical proximity to major land masses may have played some role in trans-Caribbean dispersals. Although Jamaica is now separated by a wide sea barrier from Central America, in the mid-Oligocene a major depression in sea-level (Vail *et al.* 1978) may have exposed parts of the Nicaraguan Plateau. Since the Plateau's eastern boundary lies off western Jamaica, only a short sea journey may have separated immigrating land mammals from their initial Antillean landfall. Other rafting events would still have to be invoked to account for the known distributions of primates, sloths, insectivores, and rodents in the northern and eastern islands, since Jamaica has been separated from Cuba and Hispaniola by deep (although not necessarily wide) troughs throughout the Cenozoic (Arden 1975).

Although attractive in some respects, this version of the dispersionist argument lacks the benefit of hard evidence: no one has ever found remains of these ancient transients in Jamaica. But since no one other than Anthony has made much of an effort to look for them, it remains to be seen whether this objection is fatal. The time spanned by the known mammal fauna of Jamaica is probably not more than a few tens of thousands of years, if bone-based dates of similar faunas from other locations in the Greater Antilles are a good guide (cf. Pregill 1981; MacPhee and Woods 1982). Yet sections of Jamaica have probably been positive for at least the latter half of the Cenozoic (Arden 1975; Robinson *et al.* 1977), and therefore potentially available for occupation. The extinct mammals of Jamaica must have had antecedents, and further work on the island is strongly indicated. Some major biogeographical puzzles may thereby be solved.

Acknowledgements. We thank V. Mahanger-MacPhee, R. Kay, M. K. Langworthy and C. Ray for criticism of previous versions of this paper; K. Koopman, R. Tedford and D. Webb for access to specimens; V. Krantz and A. Benson for photographic assistance; S. Gurganus, P. Thompson and M. Johnson for typing and other help; and the National Science Foundation for grants DEB-802175 (RDEM) and DEB-7811388 (CAW).

REFERENCES

- ANTHONY, H. E. 1920. New mammals from Jamaica. *Bull. Amer. Mus. Nat. Hist.* **42**, 649–475.
 — (MS.). Daily journal of expedition to Jamaica, Nov. 18, 1919 to Mar. 19, 1920. Department of Mammalogy, Amer. Mus. Nat. Hist. 220 pp.
 — 1926. Mammals of Puerto Rico, living and extinct—Rodentia and Edentata. *Scientific survey of Puerto Rico and the Virgin Islands*, **9** (2). New York Academy of Sciences, New York, 97–238.
 ARDEN, D. 1975. Geology of Jamaica and the Nicaragua Rise. In NAIRN, A. E. M. and STEHLI, F. G. (eds.). *The ocean basins and margins*, **3**, *The Gulf of Mexico and the Caribbean*. Plenum Press, New York, 617–661.
 DARLINGTON, P. J. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of mammals over water and through the air. *Quart. Rev. Biol.* **13**, 274–300.
 LANDRY, S. O. 1957. The interrelationships of the New and Old World hystricomorph rodents. *Univ. Calif. Publ. Zool.* **56**, 1–118.
 MACPHEE, R. D. E. and WOODS, C. A. 1982. A new fossil cebine from Hispaniola. *Amer. J. Phys. Anthropol.* **58**, 419–436.
 MATTHEW, W. D. 1918. Affinities and origin of the Antillean mammals. *Bull. Geol. Soc. Amer.* **29**, 657–666.
 NELSON, G. and ROSEN, D. E. (eds.). 1981. *Vicariance biogeography: a critique*. Columbia University Press, New York, 593 pp.
 PREGILL, G. 1981. An appraisal of the vicariance hypothesis of Caribbean biogeography and its application to West Indian terrestrial vertebrates. *Syst. Zool.* **30**, 147–155.
 RAY, C. E. 1964. The taxonomic status of *Heptaxodon* and dental ontogeny in *Elasmodontomys* and *Amblyrhiza* (Rodentia: Caviomorpha). *Bull. Mus. Comp. Zool., Harvard Univ.* **131**, 107–127.

- RAY, C. E. 1965. The relationships of *Quemisia gravis* (Rodentia: ?Heptaxodontidae). *Smithsonian Misc. Coll.* **149** (3), 1–12.
- RIMOLI, R. 1977. Una nueva especie de monos (Cebidae: Saimirinae: *Saimiri*) de la Hispaniola. *Cuadernos del Cendia, Univ. Aut. Santo Domingo*, **242**, 5–14.
- ROBINSON, E., LEWIS, J. F. and CANT, R. V. 1977. Field guide to aspects of the geology of Jamaica. In MATTSON, P. H. (ed.). *West Indies island arcs (Benchmark papers in geology, Vol. 33)*. Dowden, Hutchinson & Ross, Inc., Stoudsberg, Pennsylvania, 210–221.
- ROSEN, D. E. 1976. A vicariance model of Caribbean biogeography. *Syst. Zool.* **24**, 431–464.
- 1978. Vicariant patterns and historical explanation in biogeography. *Ibid.* **27**, 159–188.
- ROSENBERGER, A. L. 1977. *Xenothrix* and ceboid phylogeny. *J. Hum. Evol.* **7**, 261–281.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.* **85**, 1–350.
- 1956. Zoogeography of West Indian land mammals. *Amer. Mus. Novit.* **1759**, 1–28.
- VAIL, P. R., MITCHUM, R. M. and THOMPSON, S. 1978. Seismic stratigraphy and global changes of sea levels, part 4: Global cycles of relative changes of sea level. *Amer. Assoc. Petrol. Geol. Mem.* **26**, 83–97.
- WILLIAMS, E. E. and KOOPMAN, K. F. 1952. West Indian fossil monkeys. *Amer. Mus. Novit.* **1546**, 1–16.
- WINGE, H. 1941. *The interrelationships of the mammalian genera*. Vol. 2, *Rodentia, Carnivora, Primates*. Reitzels Forlag, Kobenhaven, 375 pp. (Trans. by Deichmann, E. and Allen, G. M.; ed. by Jensen, A. S., Sparck, R. and Volsoe, H.)
- WOOD, A. E. and PATTERSON, B. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. *Bull. Mus. Comp. Zool., Harvard Univ.* **120**, 281–428.
- WOODS, C. A. (in press). The suborder Hystricognathi. In ANDERSON, S. and JONES, J. K. (eds.). *Recent mammals of the world*, 2nd edn. Wiley, New York.
- and HOWLAND, E. B. 1979. Adaptive radiation of capromyid rodents: anatomy of the masticatory apparatus. *J. Mammal.* **60**, 95–116.

R. D. E. MACPHEE

Department of Anatomy
Duke University Medical Centre
Durham, North Carolina
U.S.A.

C. A. WOODS and G. S. MORGAN
Department of Natural Sciences
Florida State Museum,
Gainesville, Florida
U.S.A.